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THE NUTRITION OF THE EGG IN ZAMIA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LVI.

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(WITH SIX FIGURES)

FOR some time previous to the cutting off of the ventral canal cell, the central cell in most gymnosperms is surrounded by large prominent cells called the "jacket cells," which contain particularly large nuclei. The inner walls of the jacket cells, in contact with the egg, are pierced by numerous pores (*fig. 2*). During the rapid growth of the central cell the jacket cells and their nuclei are prominent; but during the period of free nuclear division in the embryo the jacket becomes less conspicuous, and finally becomes indistinguishable as a definite nutritive layer. It is evident that the jacket cells contribute to the growth of the central cells, and afterward to the growth of the egg and proembryo. The passage of various contents of the jacket cells into the egg has been described by several observers.

Goroschankin (4) says in regard to Ceratozamia: "In fresh preparations mounted in water, each canal is seen to be filled with fine protoplasm that passes over sometimes into the protoplasm of the neighboring cells and sometimes into the protoplasm of the egg cell. Transverse and longitudinal sections of fruits which were carried up with strong alcohol showed me the following: under the action of the alcohol the protoplasm of the surrounding endosperm sheath seems wholly smooth or with scarce observable projections on the side nearest the egg. But as for the protoplasm of the egg, it appears covered with projections the length of which equals nearly or wholly the length of the canals. Afterward I began to make tangential sections of the egg from alcoholic preparations. Now I was able to see the sieve plates in the canal. . . . . From my observations on the egg wall in the cycads, the following conclusions were reached:

the wall is formed of cellulose and contains a large number of canals showing genuine sieve plates, through which the protoplasm of the cells of the endosperm layers communicates with the protoplasm of the egg."

Ikeno (5) in his paper on *Cycas revoluta* says: "Since Goroschankin's researches it is known that in the cycads the protoplasm of the central cell and of the wall cells are in close connection by means of protoplasmic threads. It is easy to see that the material filling the nuclei of the wall cells, which in its natural condition is a half-fluid substance, flows out from there and goes to the central cell through these intercellular breaks. Indeed, I can find various stages of the transportation of this material to the central cell, showing as granulations in fixed material, where these granules lie just outside the nuclei, then in the protoplasmic threads themselves, then in the central cell directly before the protoplasmic break. Also one finds a large mass of these granulations at the edge of the central cell, which have collected there, evidently coming completely from the neighboring wall cells."

Arnoldi claims that the nuclei of the jacket cells pass bodily into the egg through the large pores in the inner walls of the jacket cells. In writing of *Pinus cembra* he says (2): "I can show that I could observe out of a series of sections more than one hundred and fifty nuclei passing out of the jacket cells. It is also established through my observations that the small proteid vacuoles described by Goroschankin as Hofmeister's nodules are only nuclei passing out of the jacket cells."

In writing on *Cephalotaxus Fortunei* he says (1): "In the first stages of development of the jacket cells we find the little nucleoli only half inside of the nuclei. In some later stages we find them also in the protoplasm of the jacket cells. Since these small granules are fully equal to those in the nuclei in all relations of size, staining ability, etc., since they are first observed in the nucleus and later in the protoplasm, we may conclude that they pass from the nuclei into the protoplasm. In the protoplasm of the jacket cells they are heaped up in great masses, and then pass over into the egg cell. The nodules appear in the cell on the side in which the protoplasm itself is rich in vacuoles. Observation of the passage of the granules from the jacket cells into the egg is most difficult. The egg cell and the jacket cell walls with the highest magnifications show no holes. But since on both sides of the wall we find granules of a like nature, we must admit a process of passing over. If one admit that we have not small bodies, but small drops of a·viscid fluid substance, filtration furnishes an explanation for the passing over."

Murrill (8) in his paper on Tsuga writes: "I cannot confirm for Tsuga the results of Arnoldi's recent studies (1900) on the proteid vacuoles of the Abieteae. It may be that further search on my part will reveal the passage of the nuclei of the sheath cells into the central cell, but very careful examination of numerous archegonia in all stages of development has thus far failed to show a single undoubted example of such passage. I find the nuclei of the sheath cells streaming profusely at times, as described by Ikeno (1898) for Cycas, and observe collections of granules in the outer vacuoles of the central cells which very much resemble the sheath nuclei; but the sheath cells are never found without their nuclei. The sheath remains one-layered, though its cells often divide as the archegonium grows. At points where the archegonia come into close contact, the sheath is frequently crushed and destroyed; but throughout most of its extent the cells and their nuclei continue active during the life of the archegonium."

Strasburger (6) upon re-examining Pinus failed to confirm Arnoldi's views. Margaret C. Ferguson (3) alludes to Arnoldi's study of Pinus, but fails to confirm the migration of the nuclei of the sheath cells into the egg. Land (7) in describing Thuja writes: "Protoplasmic connections between the jacket cells and the central cell were not seen, but it is possible they were overlooked owing to the extreme thinness of the dividing wall. It is not believed that the nuclei of the jacket cells pass into the central cell as reported in Caphalotaxus by Arnoldi."

Material of *Zamia floridana* was secured from Miami, Florida. The earliest stages studied showed the central cell of the archegonium before the mitosis which gives rise to the egg and the ventral canal nucleus. From this point up to the organization of embryos in which the cotyledons were beginning to appear the series was fairly complete.

During the earlier growth of the central cell no jacket is distinguishable, and during this time also the contents of the central cell are scanty and much vacuolated. As the central cell approaches its mature size and begins to fill with nutritive substances, the jacket appears and soon becomes very conspicuous its single layer of cells being rich in protoplasm, but almost destitute of starch, while the cells surrounding it are nearly filled with large starch grains (*fig. 1*, *j*, *s*). This condition continues during the later growth of the central cell, during the growth of the egg, and even during the earlier stages in the development of the embryo. During their entire period the mode by which materials pass from the jacket into the interior is the same. All the figures are from stages between the formation of the ventral canal nucleus and fertilization.

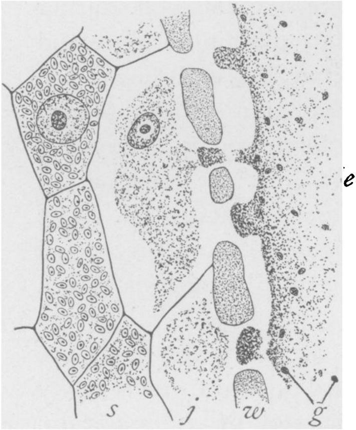

FIG. 1.—*Zamia floridana.* Portion of egg, *e*, jacket, *j*, and neighboring cells; two of the four haustoria shown are broken off; haustoria discharging contents into egg; *g*, granules passing from the haustoria into the egg; *s*, starch-containing cells outside jacket; *w*, thick inner walls of jacket cells.

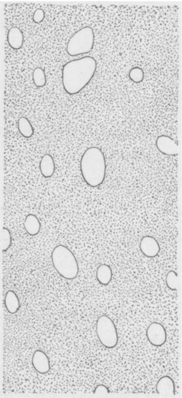

FIG. 2.—*Zamia floridana.* Portion of inner surface of jacket showing numerous pits of various sizes.

The inner walls of the jacket cells become very much thickened (*figs. 1*, *3–6*, *w*) and are pierced by numerous pores of various sizes, as shown in surface view in *fig. 2* and in section in all the other figures. Through these pits the protoplasm of the egg protrudes into the jacket cells, forming haustoria-like processes. After passing through the pits, the ends of the haustoria become distended so that the structure appears knob-shaped. The contents of the haustorium vary, and the variation is accompanied by striking variations in the staining reactions, sometimes the end of the projection appearing as a dense, deeply staining knob in which scarcely any structure can be distinguished, and sometimes staining faintly and showing beautifully the cytoplasmic reticulum. In fact, the haustorium behaves like a gland cell, during the period of accumulation staining more and more deeply, then discharging, and during the following period of exhaustion staining faintly until the active period begins again. In *fig. 1* the haustoria are discharging, the granules (*g*) coming undoubtedly from the haustoria. The appearance of the haustoria during the period of exhaustion following the discharge is shown in *fig. 3*, *h*.

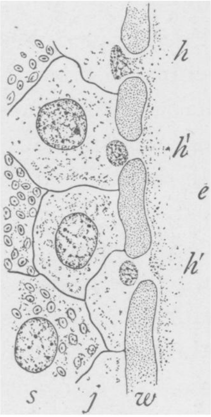

FIG. 3.—*Zamia floridana.* Period of exhaustion; *h*, haustoria; *h'*, tangential sections of the swollen ends of haustoria which might be mistaken for nuclei; *e*, peripheral portion of egg; *j*, jacket cells; *s*, starch-containing cells outside jacket; *w*, thick inner walls of jacket cells.

That the contents of the jacket cells are strongly attracted toward the haustoria is easily seen during the entire period of accumulation. In *figs. 1*, *4*, and *6* the protoplasm is shown streaming toward the haustoria, and in *fig. 4*, as is often the case, even the nucleus appears to be drawn out toward the haustorium. During the period of exhaustion (*fig. 3*) no such streaming of the protoplasm or distortion of the nuclei was observed.

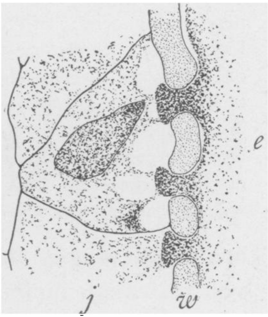

FIG. 4.—*Zamia floridana.* Streaming of cytoplasm toward haustoria; nucleus much drawn out; *e*, peripheral portion of egg; *j*, jacket cells; *w*, thick inner walls of jacket cells.

In no case was there any indication of the passage of nuclei or nucleoli from the jacket cells into the egg, and in no case did we find a jacket cell without a nucleus. However, that material is probably drawn from the nuclei as well as from the cytoplasm may be seen by comparing the nuclei of *figs. 1* and *6* with those of *fig. 3*, the former showing the active condition and the latter the exhausted condition following the discharge.

In preparations the haustoria are often broken off (*figs. 1* and *6*), and in this condition they might be mistaken for material passing in large masses from the jacket cells into the egg. This condition resembles that shown by Ikeno for *Cycas revoluta*. Possibly his figures may bear this interpretation; at least it would be worth while to re-examine Cycas with this in mind.

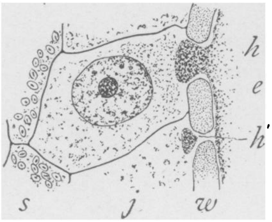

FIG. 5.—*Zamia floridana; e*, peripheral portion of egg; *h, h'*, haustoria, the lower a tangential section of the knob-like end which might be taken for a nucleolus; *j*, jacket cells; *s*, starch-containing cells outside jacket; *w*, thick inner walls of jacket cells.

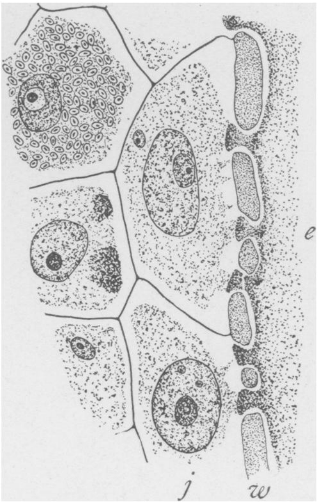

FIG. 6.—*Zamia floridana.* Streaming of cytoplasm toward haustoria; *e*, peripheral portion of egg; *j*, jacket cells; *w*, thick inner walls of jacket cells.

It often happens that the knob-like ends of haustoria are cut in a longitudinal tangential plane. In such cases they closely resemble nuclei (*figs. 3* and *5, h'*), and then they might be mistaken for nuclei passing bodily into the egg. Whether such a mistake would be sufficient to explain Arnoldi's account still remains to be seen.

No sieve plates or similar structures, as described by Goroschankin, were observed in any of the preparations.

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